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TAKEOVER ON THE TALLGRASS PRAIRIE: HOW
LESPEDEZA CUNEATA ESTABLISHES
DOMINANCE

Morgan R. Walder

31 Pages

Invasion ecology aims to study mechanisms by which invasive species are able to enter, establish, and spread within an ecosystem. This study analyzed Darwin's naturalization and the biotic resistance hypotheses as the most likely explanations for invasion by an exotic legume, *Lespedeza cuneata*, into a tallgrass prairie. Darwin's naturalization hypothesis posits that exotic species are less able to establish in communities that have related species, because similarity in morphology and function promotes intense competition for resources. The biotic resistance hypothesis states that competitors, herbivores, and pathogens already present in the community limit the colonization, naturalization, and persistence of invaders, therefore impeding invasion. Phenological and morphological data, photosynthetically-active radiation (PAR) measurements, Daubenmire cover, and biomass were recorded to test these hypotheses. As predicted by Darwin's naturalization hypothesis, *L. cuneata* mass and the mass of other legumes were negatively associated. In addition, phenological differences between *L. cuneata* and the other legumes on the study site further support Darwin's naturalization hypothesis. In order to inform conservation management, it is essential to identify mechanisms by which invasion occurs, such as was done in this study.

KEYWORDS: Invasion ecology, Invasive legume, Prairie community, Biotic resistance, Darwin's naturalization

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DOMINANCE

MORGAN R. WALDER

A Thesis Submitted in Partial
Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

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2017

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TAKEOVER ON THE TALLGRASS PRAIRIE: HOW
LESPEDEZA CUNEATA ESTABLISHES
DOMINANCE

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M.R.W.

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CHAPTER I: INTRODUCTION

The Invasive Species Problem

In the US, costs associated with invasion by exotic species are estimated at \$120 billion per year (Pimentel et al. 2005). While this estimate includes cost of eradication and control efforts, it does not include costs of important ecological effects (Catford et al. 2012). Ecological consequences of invasions include lost biodiversity (Eddy and Moore 1998), changes in ecosystem structure and function (Chapin et al 2000), and changes in biotic interactions such as competition with native species (Catford et al. 2012). Some invasive species can alter ecosystem function in just one growing season (McLeod et al. 2016), which shows how strong an impact these species can have after becoming established in a site. Such ecological effects can result in the loss of ecosystem services, which adds to the economic costs of invasive species removal or control (Catford et al. 2012).

Identifying mechanisms by which exotic plant invasions occur is essential for informed conservation management strategies. Because successful invasion is a product of ecosystem characteristics, species traits, and potential mechanisms (Williamson & Fitter 1996; Daehler 2003), the manifold combinations of these factors have resulted in a large number of hypotheses. Catford et al. (2009) identified 29 leading hypotheses about plant invasion ecology. These numerous hypotheses overlap, are redundant, and typically only focus on a single mechanism (White et al. 2006). Proliferation of hypotheses limits the ability to link findings into a broader, theoretical framework that explains these mechanisms at work. Catford et al. (2009) suggest that integrating multiple hypotheses into a broader framework, instead of creating new terms and models specific to individual systems, is more useful in gaining understanding of these mechanisms.

Invasion success is determined by three things: propagule pressure, abiotic characteristics of the area of invasion, and biotic characteristics of both the area of invasion and the invading species (Catford et al. 2009). Propagule pressure is the amount (size and number) of plant propagules that are introduced to an area and though a singular propagule could lead to the colonization of a site, continued dispersal is required for the success of the invading species. Because my focal species was established on the study site before this study began, I did not examine factors controlling dispersal. Abiotic characteristics represent constraints imposed by both geography and habitat. Biotic characteristics determine interactions within the community itself. I examined how abiotic and biotic characteristics contribute to the spread of *Lespedeza cuneata*, an invader in the Midwestern U.S.

***Lespedeza cuneata*, a Threat to Prairie Ecosystems**

Lespedeza cuneata (Dum. Cours.) G. Don (Fabaceae), also known as *Lespedeza juncea* var. *sericea*, *Lespedeza latissima*, *Lespedeza sericea*, and *Lespedeza serpens*, is a rising threat to tallgrass prairies (USDA). Common names include silky bushclover, Chinese bushclover, and sericea lespedeza. *Lespedeza cuneata* is native to Asia and Australia, and is commonly found in Korea, China, Taiwan, India, and Japan (Ohiwi 1965). This aggressive, invasive legume was introduced to the southern United States in the 1800's to help control soil erosion, and provide forage (Hoveland et al. 1961). *Lespedeza cuneata* has now been found in many areas in the United States, and has also been introduced to South Africa, Brazil, Canada, and Mexico (Hoveland et al. 1985).

Lespedeza cuneata possesses a number of traits that enable it to meet abiotic and biotic challenges. This plant is resistant to drought due to a deep taproot, produces large numbers of

small seed (3-5 mm), and grows readily in grasslands, pastures, along roadsides, and in many disturbed areas (Ohlenbusch et al. 2007). Plants grow from approximately one to five feet tall, and the closely-spaced stems become increasingly branched with age, forming dense thickets (USDA). *Lespedeza cuneata* can enter nutrient-poor sites due to its ability to fix nitrogen, and alters soil conditions through microbial communities that are established to facilitate its own growth (Coykendall and Houseman 2014, Yannarell et al. 2011). Tannins found in the leaf litter can play a large part in the soil ecosystem, and can affect germination, seedling emergence and growth, nitrogen concentration, and aboveground biomass (Langdale and Giddens 1997; Kalburtji and Mosjidis 1992).

Propagule production and dispersal have been identified as important traits enabling invasive plants to aggressively colonize new sites (Davis et al. 2000). Plants that allocate fewer resources to each seed can produce a large number of seeds, increasing the chances that some offspring will become established (Kawano 1981). These seeds are also easily transportable, which aids in easy dispersal by humans or wildlife. *Lespedeza cuneata* can produce up to 1,500 seeds per plant (Ohlenbusch et al. 2007).

In addition to vegetative spread through rhizomes (Woods et al. 2009), *L. cuneata* reproduces sexually through both out-crossing chasmogamous (CH) flowers, and self-pollinated cleistogamous (CL) flowers (Woods 2006). This flexible reproductive strategy allows *L. cuneata* to successfully surmount ecological barriers that discourage reproduction. Chasmogamous flowers are insect-pollinated, primarily by bees (Cane and Snyder 1986). If pollination is poor in a season, the plant is able to produce seeds through self-pollination. Chasmogamous flowers vary from cream to white, with the top petal having pink or purple color. Since cleistogamous flowers are self-fertilized, they have closed, non-showy petals. CH and CL flowers are scattered together

throughout the vegetative *L. cuneata* stem, with CH flowers growing in clusters from the axis of the leaf. At peak flowering time, chasmogamous flower production by *L. cuneata* is >20X, 3X more seed per ramet, and 5X more seed per plant than that of native *Lespedeza* species (Woods et al. 2009). Due to the large number of flowers attracting pollinators, *L. cuneata* can experience greater seed set when compared to native congeners *Lespedeza capitata*, *Lespedeza violacea*, and *Lespedeza virginica* (Woods et al. 2009).

Hypotheses and Predictions

Based on the traits of *L. cuneata* and characteristics of the study site, I selected two hypotheses to test using field-collected data: Darwin's naturalization hypothesis and the biotic resistance hypothesis. Additional alternative hypotheses are discussed later in this paper.

The limiting similarity hypothesis is also known as Darwin's naturalization hypothesis and thus this name will be utilized in the following text. Darwin's naturalization hypothesis states that an exotic species is less likely to establish in communities with related species because similarity in morphology and function among taxonomically related species would promote intense competition for resources (Darwin 1859; MacArthur and Levins 1967; Callaway and Ridenour 2004; Hierro et al. 2005). This hypothesis predicts a negative correlation between abundance of exotic species and the total abundance of related species. In addition, it predicts that co-occurring species should differ in life history, morphology, and function. If this hypothesis applies to *L. cuneata* in a prairie community, I predict that there should be a negative correlation between the abundance of *L. cuneata* and other legumes. I further predict that *L. cuneata* should differ in life history, morphology, and function than other co-occurring legumes.

The biotic resistance hypothesis states that competitors, herbivores, and pathogens already present in the community limit the colonization, naturalization, and persistence of newcomers, therefore impeding invasion (Levine et al. 2004; Parker and Hay 2005; Alpert 2006). This hypothesis assumes that species new to a site are not adapted to competitors in the new range and are not defended against damage from novel pathogens and herbivores. Studies of restored prairies provide support for this hypothesis (Foster et al. 2015). Restored plots, which had greater native prairie plant species and total plant cover, as well as increased species richness and diversity, showed less non-prairie species cover than plots that had not been restored. Foster et al. (2015) showed that *L. cuneata* cover was decreased by restoration efforts but increased in plots that had not been restored. If the saturation of the community leaves few resources available for use, as posited by the biotic resistance hypothesis, I predict that invasion by *L. cuneata* is negatively associated with the number or total cover of species found in an experimental plot.

Research Goals

This study focused on factors that allow *L. cuneata* to successfully spread within a community. My overarching hypothesis is that multiple life history traits allow *L. cuneata* to utilize nutrient-poor, sparsely vegetated sites, and suppress the growth of the native species. Through detailed observations and quantification of life-history traits and analysis of cover and aboveground biomass, I tested which of two hypotheses better explains the success of this invasive legume. Finally, I considered whether alternative hypotheses may better explain the rapid spread of *L. cuneata*.

CHAPTER II: MATERIALS AND METHODS

Field Site

John English Prairie is a reconstructed prairie in Comlara Park, McLean County, IL, USA (40.621388, -89.014729). This site was agricultural land over 40 years ago. John English Prairie is located near the southern part of Evergreen Lake, which borders the prairie on the west side, and an agricultural field on the east side. This reconstructed prairie is generally burned annually in the spring, and in the year of data collection (2015) it was indeed burned in March.

To take advantage of existing background data, I conducted my observations in experimental plots originally established as part of a manipulative study on hemiparasites (Borowicz and Armstrong 2012). At the time of establishment, *Pedicularis canadensis* was present in each of the 96, 1-m² experimental plots. One of eight treatments were randomly assigned to each plot. These were combinations of three factors: parasitic plants (no removal/removed in the spring), soil fertility (no addition/ annual addition of granular 10-10-10 N-P-K fertilizer), and shade (full sun/50% shade June-October). The shade treatment was discontinued in 2010. These plots were distributed within 12 spatial blocks. Valuable background data from each plot include the years when *L. cuneata* was observed, biomass of native graminoids, non-legume forbs (henceforth “forbs”), *L. cuneata*, and other legumes harvested in 2008, biomass of *L. cuneata* in 2009, and the number of species present in 2009.

Data Collection

Starting in May 2015 and continuing weekly throughout the growing season (May-October 2015), detailed phenological and morphological data were taken on *L. cuneata* and other species in the plots to determine: (1) timing of flowering, (2) height of the plant, and (3) total

number of flowering stems. The tallest flowering individual of each species in the experimental plot was chosen for measurements for that week. Flowering times within a plot were considered to have begun when one individual of a species had begun flowering and ceased when no individual representatives of that species were in flower.

Three mature specimens per species were collected and aboveground biomass was measured in order to quantify differences in size of the legumes in our prairie community. For each species, samples were randomly selected by running a ten meter transect from a plot, used in the previous study, containing that legume species. The closest specimen to a randomly-chosen number on the transect was collected and used for analysis. Legumes present on the study site included: white clover (*Trifolium repens*), white wild indigo (*Baptisia alba*), purple prairie clover (*Dalea purpurea*), white prairie clover (*Dalea candida*), round-headed bushclover (*Lespedeza capitata*), and silky bushclover (*Lespedeza cuneata*). These specimens were collected after flowering, and then dried at 60 degrees Celsius for one week and weighed to determine total aboveground dry mass.

Photosynthetically-active radiation (PAR) levels at the ground level were taken in June 2015 to compare how *L. cuneata* and other species attenuate the light. One measurement was taken interior on each side of the experimental plot (50 cm) and then the four measurements were averaged in order to get one value for each experimental plot. Measurements were taken on cloud-free days in the late morning and early afternoon between 11am-2pm.

During the growing season in July 2015, cover (Daubenmire 1959) was determined in each plot in order to evaluate the effects of fertilizer and removal of the hemiparasitic plant *P. canadensis* on abundances of *L. cuneata* and functional groups of native species (grasses, non-legume forbs, and legumes). In addition, each plot was inventoried to determine effects of

treatments on species richness. This survey work allowed me to document the presence of rarer species.

In October 2015, all aboveground biomass was harvested in the northwest 0.25-m² corner of the 1-m² experimental plot. It was then separated into *L. cuneata*, graminoids, *P. canadensis*, other forbs, and remaining legumes. The biomass was then dried at 60 degrees Celsius for one week and weighed to determine the dry mass (g. 0.25 m⁻²).

Statistical Analyses

A principal component analysis (PCA) was used to examine how current community characteristics affect the aboveground biomass of *L. cuneata* in 2015. PCA was used to produce uncorrelated variables that characterized the plant community in the experimental plots. The original values for each plot were: the numbers of C₃ grass species, C₄ grass species, non-legume forb species, legume species other than *L. cuneata*, exotic species, weedy species, and the measure of photosynthetically-active radiation at ground level. The United States Department of Agriculture (USDA) was utilized to determine which species were considered weedy. Principal components with eigenvalues greater than one were retained for analysis. These scores for community characteristics were included with fertilizer treatment, spatial blocking, and hemiparasite removal as main effects in an ANCOVA to determine which factors significantly affect *L. cuneata* mass in the sampled portion of the plots.

In order to characterize the six legume species found on our study site, shoot length (cm) and aboveground dry mass (g) were response variables in a MANOVA to determine differences among the species.

The final two analyses examined how the community present several years earlier affected establishment and growth of *L. cuneata*. First, using only plots from which *L. cuneata* was absent in 2009, a logistic regression tested whether the number of species in the plots in 2009 (= species richness) affected subsequent establishment of *L. cuneata*. Then, a multiple regression was run on the entire data set (including plots with and plots without *L. cuneata* in 2009) in order to further analyze invasion by *L. cuneata*. For this analysis the response variable was the log-transformed *L. cuneata* mass in 2009 subtracted from the log-transformed mass in 2015. Thus a larger positive value indicates greater growth. Species richness and biomass of each of the functional groups from 2009 (graminoids, non-legume forbs, hemiparasite *P. canadensis*, and legumes other than *L. cuneata*) were independent variables.

CHAPTER III: RESULTS

The principal component analysis provided a better understanding of the characteristics of the contemporary community that are associated with the success of *L. cuneata*. The first three principal components from analysis of the prairie community explained approximately 71% of the variance in the measurements from the plots (Table 1) and were included in the ANCOVA. The first principal component was strongly and positively associated with the number of non-legume forb species and the number of weedy species. The second principal component was positively associated with the number of other legume species and PAR at ground level. The third principal component was positively associated with number of C₃ grasses. ANCOVA indicated that factors loading strongly on principal component two were strongly and negatively associated with *L. cuneata* mass ($F_{1,78} = 11.17$, $P = 0.0013$). Mass of *L. cuneata* decreased as available light and the abundance of legumes (excluding *L. cuneata*) increased (slope=-0.261, se= 0.084). The first and third principal components, which were associated with numbers of C₃ and C₄ grasses, forbs, weedy species, and exotic species in the community, were not associated significantly with *L. cuneata* biomass ($P > 0.05$ for both). Spatial block ($F_{11,78} = 5.33$, $P = <0.0001$) and fertilizer ($F_{1,78} = 6.87$, $P = 0.0105$, Fig. 1) were significant effects. Plots that received the fertilizer treatment had lower amounts of *L. cuneata* mass than plots that did not receive the fertilizer treatment, consistent with findings (Brandon et al. 2004). Absence of fertilizer resulted in a higher biomass of *L. cuneata*.

Table 1. Results of principal components analysis. Factors 1 through 3 explained approximately 71% of the variance in the measurements. Forbs and weedy species load heavily onto Factor 1. Photosynthetically-active radiation (PAR) and all legumes other than *Lespedeza cuneata* load onto Factor 2. C₃ grasses load onto Factor 3.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
C ₃ Grasses	0.11639	0.04863	0.95373	-0.00631	0.16197
C ₄ Grasses	-0.06143	0.07459	0.00098	0.98780	0.09996
Forbs	0.81366	0.30136	0.30746	-0.05825	0.04420
Legumes (except <i>L. cuneata</i>)	0.14677	0.78069	-0.10863	0.05398	0.48991
Exotic Species	0.36415	0.04998	0.39699	0.17657	0.75233
Weedy Species	0.90853	0.05908	-0.03434	-0.03582	0.26481
PAR 2015	0.15902	0.89806	0.13925	0.06246	-0.12128

Fig. 1. Mean ($\pm$ se) *L. cuneata* dry mass collected from fertilized and non-fertilized plots in 2015.

MANOVA revealed highly significant differences in shoot mass and length among the legume species (Pillai's Trace, $F_{10,24}=27.59$, $P<0.0001$, Fig. 2). The larger magnitude of the standard canonical coefficient (length = -1.0584, mass = 4.9453) indicated that mass explained more of the variation among species than did shoot length and the opposite signs indicate the mass and length tend to be negatively correlated. Two species, *L. cuneata* and *Baptisia alba* (White Wild Indigo), stand out from the other legumes. *B. alba* is high in mass, whereas *L. cuneata* has greatest allocation to length.

A flowering phenology (Fig. 3) produced with phenological data shows beginning and ending of flowering for all species found in experimental plots. *L. cuneata* is among the last of all species, and the last legume, to flower on the study site. In addition, *L. cuneata* flowers over a month later than its congener, *L. capitata*. The flowering of *L. cuneata* overlaps with few species and no legumes on our field site.

Fig. 2. Mean shoot length and mean dry mass of the six legume species present on the study site. Bars indicate standard errors. White clover and silky bushclover are non-native legume species found in experimental plots on John English Prairie.

Fig. 3. Flowering times of species within experimental plots on John English Prairie study site.
(green= graminoids, blue=legumes, purple=forbs)

By 2009, *L. cuneata* had invaded 29 of the 96 experimental plots, and all 96 plots were invaded by 2015. The logistic regression showed that species richness in the plots without *L. cuneata* in 2009 did not significantly affect entry by *L. cuneata* into these plots by 2015 (Wald $\chi^2_{(1)} = 1.8158$, $P=0.1778$). Plots with a small number of species in this year were no more likely to have *L. cuneata* present by 2015.

Likewise, species richness in 2009 did not significantly affect change in *L. cuneata* biomass between 2009 and 2015 ($P=0.3717$). However, forbs ($P=0.0096$) and legumes ($P=0.0245$) were negatively correlated with the growth of *L. cuneata*. Plots that had a greater mass of these two functional groups in 2008 showed less growth of *L. cuneata* in 2015. By contrast, graminoids significantly and positively affected *L. cuneata* ($P=0.0130$), meaning that the more grass present in a plot in 2008, the more growth of *L. cuneata* by 2015. The hemiparasite *Pedicularis canadensis* had no significant effect on *L. cuneata* growth ($P=0.1837$).

CHAPTER IV: DISCUSSION

This study focused on two hypotheses that were possible explanations for the invasion and spread of *Lespedeza cuneata* in a tallgrass prairie community. Darwin's naturalization hypothesis postulates that exotic species are less likely to establish in communities with related species because similarity in morphology and function promotes intense competition for resources. The Darwin's naturalization hypothesis generally was supported by this study, as the mass of *L. cuneata* and the mass of other legumes were negatively associated. Furthermore, phenological differences between legumes on our study site and *L. cuneata* provide more evidence in support of this hypothesis.

The assumption that invaders are less successful in communities with more species, as stated by the biotic resistance hypothesis, generally was not supported. This hypothesis postulates that species-rich communities have more effective competitors, herbivores, and pathogens, and use resources efficiently, thus leaving no room for invaders. However, my results show that *L. cuneata*'s invasion had no increased success when invading plots that had fewer potential competitors.

Darwin's Naturalization Hypothesis

Darwin's naturalization hypothesis predicts a negative correlation between *L. cuneata* and other legumes because the similarity in morphology and function of related species would promote competition for resources (Darwin 1859; MacArthur and Levins 1967; Hierro et al. 2005; Pearson et al. 2012). Consistent with prediction, my results show that the mass of *L. cuneata* decreased as the functionally similar legumes on the study site increased. In addition, observations showed that *L. cuneata* is significantly different from the other legume species

located on our field site in both shoot length and mass. *L. cuneata* has a high allocation to shoot length, whereas other species such as *B. alba* have greater allocation to mass.

All legumes, including *L. cuneata* are nitrogen-fixing, so they play the same functional role within a community, as well as being phylogenetically related. How then, does *L. cuneata* invade a community that includes these other legume species? Differences between *L. cuneata* and native legumes in terms of phenology, seed production, morphology, and chemistry may help to answer this question. *Lespedeza cuneata* is among the last species and is the last legume to flower on the study site. *L. cuneata* flowers a little over a month later than its native congener, *L. capitata*. Since *L. cuneata* flowers later than other legumes, it avoids competition for pollinators with those species. However, if flowering time for these species did overlap, it is likely that *L. cuneata* would still be successful. Even though both *Lespedeza* species exhibit both flower types, *L. cuneata* has an advantage over its native congener, *L. capitata*. At peak flowering time, chasmogamous flower production by *L. cuneata* is >20X that of native *Lespedeza* species (Woods et al. 2009). Due to the large number of flowers produced that attract pollinators, *L. cuneata* benefits from pollination more than its native *Lespedeza* congeners (Woods et al 2009). When the invasive *L. cuneata* was compared with three native *Lespedeza* species (*L. capitata*, *L. violacea*, and *L. virginica*), insect visitation rates were higher per plant on *L. cuneata* than on the native congener species (Woods et al. 2012). *Lespedeza cuneata* was a strong competitor for pollinators with *L. capitata* and *L. violacea*, which had fewer shared pollinators (Woods et al. 2012).

Greater production of flowers and attraction of pollinators can increase propagule pressure and population growth. A life table response experiment showed that when compared to *L. virginica*, *L. cuneata* produced more seeds with higher germination. The majority of *L.*

virginica seeds stay in the seed bank, whereas the seeds of *L. cuneata* germinate very quickly, which allows for a quicker population growth of *L. cuneata* (Schutzenhofer et al. 2009). Thus, once it successfully establishes, *L. cuneata* has great potential to proliferate.

Lespedeza cuneata exhibits a growth form and chemistry distinct from other legumes on the site. *L. cuneata* allocates greater biomass to leaves, resulting in a higher total leaf area, compared to *L. capitata* (Smith and Knapp 2001). This is consistent with studies that have found exotic species have a higher specific leaf area, compared to native plants (Allred et al. 2010; Baruch and Goldstein 1999; Lake and Leishman 2004). Higher specific leaf area shades out species below and allows for greater light absorption. *Lespedeza cuneata* grows tall, coarse stems that form dense stands, a characteristic unlike other legumes growing on the field site. These dense stands limit the amount of light available to the species underneath, thus shading them out (Brandon et al. 2004; Reinhart et al. 2006). *Lespedeza cuneata* has tannin-containing allelopathic leaf litter, which no other co-occurring legumes produce (Langdale and Giddens 1967, Kalburtji and Mosjidis 1992). This tannin-containing leaf litter has the potential to suppress or inhibit its native competitors (Callaway and Ridenour 2004; Hierro et al. 2005). Thus, once established, *L. cuneata*'s distinctive growth form and chemistry may provide a competitive edge over native species. Experiments showing the affects of this tannin-containing litter on co-occurring species is discussed in depth with the novel weapons hypothesis in following pages.

Biotic Resistance Hypothesis

Overall, the biotic resistance hypothesis, which predicted that *L. cuneata* would be negatively associated with the number of species present in the plot, was not supported. Using

species richness as an index of community diversity, there was no trend of *L. cuneata* more successfully invading plots with fewer potential competitors. This is consistent with results of another study that suggests species identity is more important than species richness (Crawley et al. 1999). While species richness was found unimportant in terms of invasion, perhaps the sheer mass of individuals present does matter. *L. cuneata* was less successful in plots with greater mass of forbs and legumes, which suggests that dense plots are potentially more resistant to invasion. The mass of graminoids was positively associated with *L. cuneata*, most likely due to the intense competition that occurs with forbs and legumes. Where grass is low, forbs and legumes are more abundant, thus reducing the growth of *L. cuneata*.

Fertilizer reduced the growth of *L. cuneata* biomass, even though the treatment led to greater overall plot biomass (Borowicz and Armstrong 2012). Although nitrogen fixation gives *Lespedeza cuneata* an advantage over non-legume species in non-fertilized plots, when plots are fertilized, the co-occurring species are given the resources necessary to compete with *L. cuneata*.

Possible Contending Hypotheses

The method of multiple working hypotheses is based on the idea that several hypotheses can be correct in explaining a phenomenon (Elliott and Brook 2007). There are more hypotheses that can explain how *L. cuneata* spreads throughout a system than the two hypotheses that were analyzed in this study. Described below are some hypotheses that can also potentially explain the invasion of *L. cuneata* in a system.

The ideal weed hypothesis describes life history characteristics and traits of the invasive species that allow them to outcompete the native species, thus facilitating invasion (Rejmanek and Richardson 1996; Sutherland et al. 2004). Sutherland et al. (2004) identified plant life

history characteristics for non-weedy species, native weeds, non-native weeds, and non-native invasive weeds. Invasive weedy species were less likely to be forbs, and more likely to be perennial, monoecious and self-incompatible than non-invasive species (Sutherland et al. 2004). Consistent with this description of invasive, non-native species, *L. cuneata* is a monoecious, perennial legume. However, *L. cuneata* produces both outcrossed chasmogamous and self-pollinated cleistogamous flowers, which does not agree with the findings of Sutherland et al. (2004). Nonetheless, this self-compatibility enables a single plant to proliferate in a new area, and could explain the success of *L. cuneata* at our study site.

Disturbance to a community can alter the structure and function, allowing invasive species the opportunity to colonize and establish in the disturbed area (Sher & Hyatt 1999; Hood & Naiman 2000; Colautti et al. 2006). The removal of *Pedicularis canadensis* in experimental plots could act as a disturbance event if the empty space caused by this removal allows *L. cuneata* the opportunity to establish, in addition to escaping the effects of the hemiparasite. However, we see that this is not the case, assuming that the removal treatment acted as an actual disturbance to the community. When the removal treatment of *P. canadensis* was included in our various statistical analyses, it was non-significant. This shows that in plots that were disturbed due to removal of *P. canadensis*, *L. cuneata* did not show increased establishment. From our results, we would reject this hypothesis as being a possible explanation for the spread of *L. cuneata* at our site.

The evolution of increased competitive ability (EICA) hypothesis posits that the lack of natural enemies allows the invasive species to allocate resources to functions that will allow it to be more competitive in its invaded range, instead of using those resources to combat enemies (Blossey & Notzgold 1995; Callaway and Ridenour 2004; Joshi and Vrieling 2005). We would

predict that in its introduced range, *L. cuneata* should exhibit reduced defenses against its native enemies, and invest more in traits that allow greater competition with native species. When comparing the ancestral genotype of *L. cuneata* introduced in 1930, with the modern-day North American invasive and with native Japanese genotypes, the North American invasive genotype outcompeted both the Japanese native and ancestral genotypes (Beaton et al. 2011). The invasive North American genotype exhibited greater aboveground biomass than the other genotypes, thus showing that it less affected by its competitors (Beaton et al. 2011). This study suggests that *L. cuneata* exhibits increased competitive abilities when introduced into a new range.

Novel weapons are allelopathic chemicals which invasive species can release that can increase invasion success against native species not adapted to these chemicals (Callaway and Ridenour 2004; Hierro et al 2005). *Lespedeza cuneata* has tannin-containing leaves that fall to the ground in the form of litter (Corbett 2010). Residues of *L. cuneata* stems reduced growth in corn, which then led to the further investigation of this novel weapon (Langdale and Giddens 1967). A study investigating the effects of *L. cuneata* residues on warm-season grasses showed that the residues had a negative effect on bermudagrass (*Cynodon dactylon*) and bahiagrass (*Paspalum notatum*) growth, but did not affect the germination or seedling emergence of either species (Kalburtji and Mosjidis 1992). Kalburtji and Mosjidis (1993) followed with another study to examine the effects of *L. cuneata* residues on cool-season grasses. Greenhouse experiments showed that germination, emergence of seedlings as well as seedling growth, nitrogen concentration and aboveground biomass of tall fescue (*Festuca arundinacea*) were reduced. In addition, aboveground biomass and nitrogen concentration in ryegrass (*Lolium multiflorum*) were reduced by *L. cuneata* residues. The addition of nitrogen fertilizer compensated for negative effects on both species. This suggests that the addition of nitrogen may

be needed to enhance growth that would otherwise be curtailed by the residues from *L. cuneata* (Kalburtji and Mosjidis 1993). Dudley and Fick (2003) found that when exposed to stem and leaf residues, none of the grasses tested showed any reduction in growth. However, germination rates were reduced for several of the species tested including big bluestem (15-27% reduction), Indian grass (25-39% reduction) and Kentucky bluegrass (47-60% reduction). This suggests that while growth of these grasses may not be affected, the success of germination is. Little bluestem was in no way affected by *L. cuneata* residues (Dudley and Fick 2003). The results of these studies show that there is a no agreement when it comes to reporting the effect of allelopathic chemicals in *L. cuneata* on other species. While this question has been tested on a limited number of grasses, the results vary widely. From only an effect on growth and no germination or emergence effects to no effect on growth and a reduction in germination, we see that more studies need to be carried out on this topic. There is a lack of consensus surrounding this hypothesis in relation to *L. cuneata*.

Recommendations for Management

Darwin's naturalization hypothesis suggests increasing the abundance of native species (Catford et al. 2009). Greater mass of legumes seems to afford some resistance to invasion, or at least limits the rate of invasion growth. For this reason, increasing plantings of native legumes in tallgrass prairie restoration and reconstruction efforts could keep invasive legumes at bay.

Annual burning of tallgrass prairies scarifies the seed of *L. cuneata* thus enhancing its germination (Cummings et al. 2007). If the management goal is to eradicate *L. cuneata* as quickly as possible, annual burning in the spring will more rapidly deplete the massive seed bank that *L. cuneata* creates. If proper continued management is not carried out in the correct

timeframe, denser stands of *L. cuneata* will form, thus adding to the invasion. Correct application of herbicide to kill the resprouted *L. cuneata* seedlings would keep increasing invasion at bay, as spring burning increases the establishment of *L. cuneata*. Alternatively, growing season prescribed fire carried out in the summer would reduce seed set for that year. Growing season prescribed fire will only be successful if the site is not previously spring burned, as thatch and litter are imperative for ignition.

CHAPTER V: RELEVANCE AND CONCLUSIONS

Due to the significant damage that invasive species can cause, studies of their interactions within natural communities are vital in order to inform conservation efforts. In Illinois, exotic species are of particular threat to the tallgrass prairie, an ecosystem that has experienced significant decline in area throughout the state (Noss et al. 1995). Tallgrass prairies have become highly fragmented in Illinois, with 0.01% of the original prairie remaining (Samson and Knopf 1994). In prairie reconstructions that are carried out on degraded agricultural fields, exotic species can invade and dominate quickly (Goldblum et al. 2013).

Identifying mechanisms by which invasion occurs is essential for informing conservation management strategies. At the John English Prairie field site, the *L. cuneata* invasion is beyond the possibilities of eradication. For systems that have been so heavily invaded such as my field site, only control and management efforts are feasible. It is sad to see a reconstruction effort, such as the one carried out on John English Prairie, fall prey to such an aggressive, uncontrollable invasive species.

Further studies are needed to evaluate more hypotheses related to *L. cuneata* in order to complete the story of its mechanisms of successful invasion. This study has provided valuable information that will aid management efforts in the future.

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